

## Taxonomic Revision of the Common Indo-West Pacific Nudibranch *Phyllidia varicosa* Lamarck, 1801

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**Abstract.** There has been a long-lasting debate on the taxonomic status of *Phyllidia varicosa* Lamarck, 1801, lacking a black foot stripe in preserved condition, and *P. arabica* Ehrenberg, 1831, retaining such a stripe after fixation. The present study demonstrates the significant influences of preservation on phyllidiid color patterns. Twenty-six *P. varicosa* specimens from Indonesia were fixed and stored under exactly the same conditions. While some specimens hardly faded at all, others completely lost their black pigmentation. Since living phyllidiids resembling *P. varicosa* all possess a foot stripe, its absence in a few preserved specimens described in the literature is easily explained as preservation artifacts. Still having faded remainders of a dark foot stripe, the recently rediscovered holotype of *P. varicosa* proves the synonymy of *P. varicosa* and *P. arabica*. In a detailed redescription, *P. varicosa* is shown to display considerable external and anatomical variability. Differences from *Phyllidia alyta* Yonow, 1996, from the Indian Ocean, of which type material has been reexamined, are critically discussed.

### INTRODUCTION

The status of the very common and conspicuous Indo-West Pacific species *Phyllidia varicosa* Lamarck, 1801, has been subject to considerable dispute during recent years. The reason for all subsequent confusion was the description of a single specimen, on the basis of which Cuvier (1797) established the genus *Phyllidia* and which has been considered lost since 1866 (Willan et al., 1998). Lamarck (1801) introduced the specific name *varicosa* for the specimen described but not named by Cuvier. Both early authors in their descriptions neither mentioned a black longitudinal line on the foot sole nor did Cuvier (1804) show such a stripe in his drawings of the same specimen later (as *Phyllidia trilineata* Cuvier, 1804). On this basis, Yonow (1986, 1988, 1996) separated *P. varicosa* without a black foot stripe from the otherwise identical *Phyllidia arabica* Ehrenberg, 1831, having a black stripe. In contrast, Brunckhorst (1993) considered *P. arabica* as a synonym of *P. varicosa* which was confirmed by the recent rediscovery of the holotype (Willan et al., 1998). A number of very faint dark dashes on the foot sole was suspected to be the result of artificial fading. Doubting the possibility of extensive fading of the black pigment due to preservation, Yonow (1996) used the detailed appearance of the black foot stripe as a main char-

acter to distinguish the new species *Phyllidia alyta* Yonow, 1996 from *P. varicosa*.

The present study shows that some specimens of *P. varicosa* may fade so much due to preservatives that the black pigmentation on the dorsal and ventral surfaces, including the stripe on the foot sole, disappears completely. Notes on the variability of the external morphology and a detailed anatomical description of *P. varicosa* are given. In addition, *P. varicosa* is compared with the similar species *Phyllidia alyta*.

### MATERIALS AND METHODS

A total of 27 specimens of *P. varicosa* ranging in length from 12 mm to 56 mm were examined. Twenty-six specimens were collected by A. Fahrner in September 1994 in Indonesian waters, at Lovina Beach/Bali (two specimens), Gili Trawangan/Lombok (22 specimens), and Gili Meno/Lombok (two specimens). Specimens were found, mostly by using SCUBA, on coral reefs in depths between 2 and 21 m. They all were treated in exactly the same way and with the same chemicals: they were anesthetized by slowly adding 20% MgCl<sub>2</sub> to the seawater, fixed in 10% buffered formalin and seawater for 24 hours, and preserved in 70% ethanol. One additional specimen from the Red Sea (Dahab, Egypt, October 1997, reef lagoon) was just fixed in 4% seawater buffered formalin.

Twenty-five voucher-specimens were deposited in the Zoologische Staatssammlung München (ZSM, Nos. 19983418–32). The external morphology, especially the color patterns of the foot sole, and anatomical features of seven dissected specimens were investigated in detail under the binocular dissecting microscope. In addition, 14 specimens of *Phyllidia alyta* from the British Museum of Natural History (BMNH Nos. 1996107–8, 1996315–23), including the holotype and two paratypes, and a recently collected specimen from the Maldives (February 1999; ZSM No. 19991170) were studied. Finally, 102 preserved specimens of 17 other phyllidiid species, collected together with the Indonesian *P. varicosa* specimens, were examined in order to compare the reaction of the color pigments to the preservatives in which the animals are stored. The central nervous system of one *P. varicosa* specimen was critical-point dried for scanning electron microscopy (SEM).

## SYSTEMATICS

### Phyllidiidae Rafinesque, 1814

#### *Phyllidia* Cuvier, 1797

#### *Phyllidia varicosa* Lamarck, 1801

*Phyllidia varicosa* Lamarck, 1801:66; Bruckhorst 1993:26–29, figs. 2, 4–6, 23, 24, pl. 1 A–D.

*Phyllidia trilineata* Cuvier, 1804:268, pl. A, figs. 1–6.

*Phyllidia arabica* Ehrenberg, 1831:pages unnumbered.

For an extensive synonymy of *Phyllidia varicosa* see Bruckhorst (1993), and slight modifications by Willan et al. (1998).

**External morphology (Figures 1A–F, 2A, B):** The living and freshly preserved specimens from Indonesia in 1994 all fit precisely the description of *P. varicosa* given by Bruckhorst (1993), including the presence of a median black stripe on the foot sole. Three blue-grey tubercle ridges between four longitudinal black lines and yellow-capped tubercles characterize the dorsum of this species. In the examined specimens, the color patterns of the dorsum show a remarkable variability. The tubercle ridges may be continuous (Figure 1A) or broken (Figure 1C) and the four longitudinal black lines may be all connected (Figure 1C), all isolated (Figures 1A, 2A) or just two lines may touch (Figure 1E). Ventrally, the anterior edge of the foot is notched in 23 specimens and concave in three specimens.

After four years of storage in ethanol, the Indonesian specimens differ considerably in the state of preservation of the color pigments (Table 1). Twelve specimens retain all the black and grey pigmentation both dorsally and ventrally (Figure 1C–F). They are hardly faded at all; only the yellow-orange of the tubercles and rhinophores is lost. Another six specimens still show a very distinct color pattern on the dorsal surface and also a distinct black stripe on the foot sole. However, the dark grey color

of the gills and the foot sole of these specimens gave way to a cream-white. Three specimens are more faded ventrally and have lost parts of the foot stripe (Figure 2A, B). One specimen is very faded dorsally and ventrally, and the foot stripe is very indistinct. Finally, four specimens lack a line on the sole of the foot, and two of these specimens are so faded that all the black and grey coloration dorsally and ventrally disappeared completely (Figure 1A, B). These two specimens already in life were lighter colored than the other collected *P. varicosa* specimens. Of the 22 preserved *P. varicosa* specimens retaining black markings on the foot sole, 12 are characterized by an unbroken, continuous line (Figure 1D, F), while 10 show different stages from a slightly broken to a distinctly broken or dotted stripe.

The single *P. varicosa* specimen from the Red Sea differs from the Indonesian specimens in having fewer black rays and marks on the mantle margin. The four longitudinal stripes on the dorsum are not connected, and the three tubercle ridges are continuous. It is remarkable that this specimen lost its black stripe on the foot sole completely within less than 1 year of preservation, while the dorsal black pigmentation is hardly faded at all.

Among 17 other phyllidiid species that have been investigated within the framework of this study (see also Fahrner & Beck, in press), a total of eight specimens of *Phyllidia elegans* Bergh, 1869; *Phyllidiella pustulosa* (Cuvier, 1804); *Phyllidiopsis striata* Bergh, 1889; *Phyllidiopsis annae* Bruckhorst, 1993; and an undescribed species of *Fryeria* (Fahrner & Beck, in press), have lost all black pigmentation and faded entirely.

### Anatomy

**Digestive system (Figures 3A, B, 4):** The foregut lacks any distinctive markings. A short, thin-walled oral tube is leading to the thick musculo-glandular pharyngeal bulb which has about the same length as width. Cream-colored bodies of the oral glands cover the postero-ventral, and in few specimens also the postero-lateral and postero-dorsal parts of the pharyngeal bulb. Two retractor muscles arise posterodorsally on the pharyngeal bulb and insert the dorso-lateral body wall. These muscles are wide bands splitting into smaller bundles at their origin at the pharyngeal bulb. The pharynx shows considerable variability in *P. varicosa*. After a short “intrabulbous” portion, a more or less swollen, tubular pharynx leaves the pharyngeal bulb posterodorsally, immediately forming a loop to the anterior-right in four specimens examined anatomically (Figure 3A). In three specimens the pharynx also leaves the pharyngeal bulb posterodorsally but then extends posteriorly, turns and runs back anteriorly and turns a second time, thus forming an “S” in lateral view (Figure 3B). The esophagus narrows, passing through the central nerve ring (Figure 4), continues straight backward, and from anteriorly opens into the holohepatic,

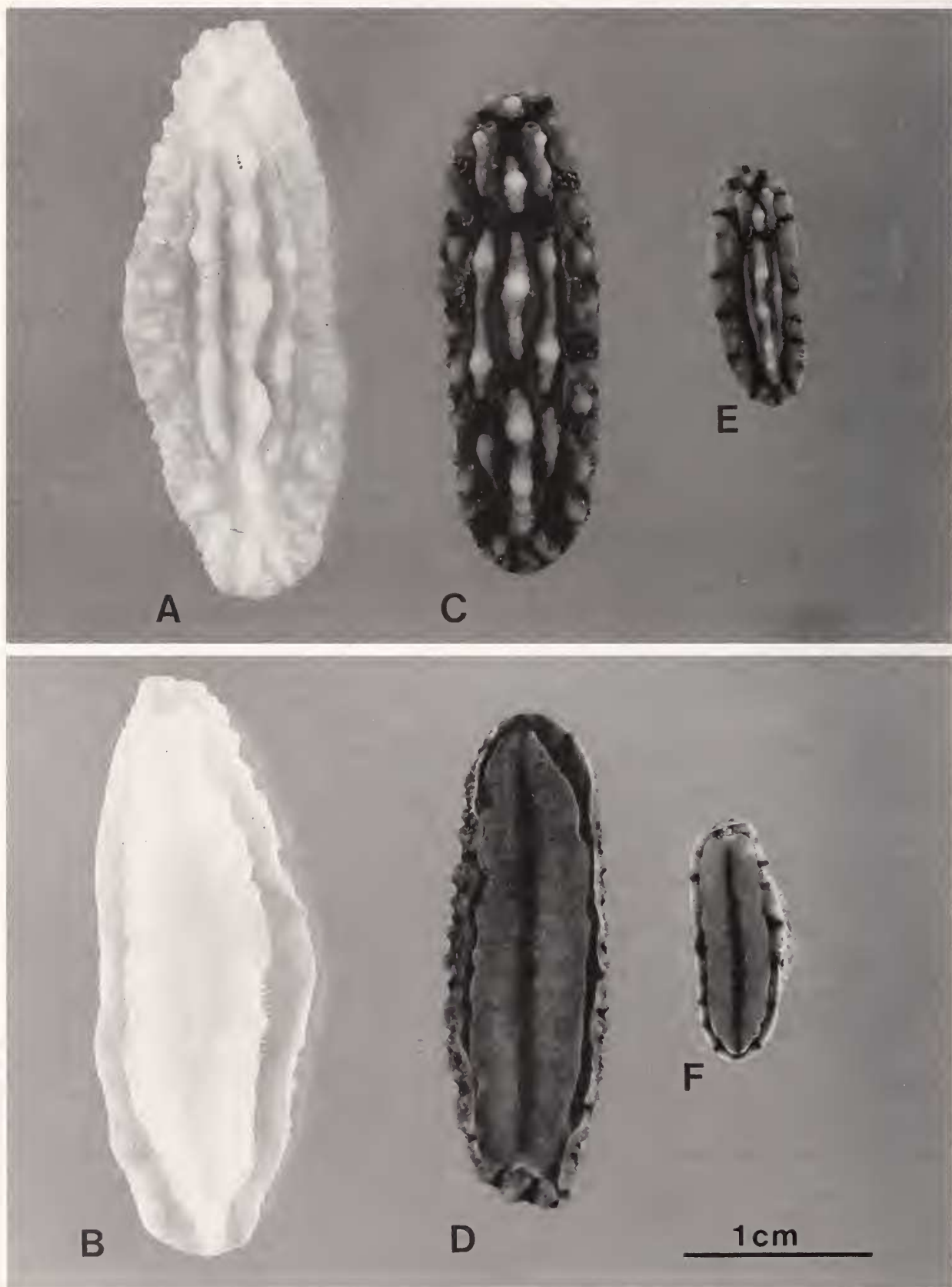




Table 1

*Phyllidia varicosa*: State of preservation of the color patterns of 26 specimens from Indonesia collected in 1994.

No. of specimens	Dorsal coloration (black and blue-grey)			Ventral coloration (light and dark grey)			Stripe on foot sole		
	Entirely faded	Faded	Hardly faded	Entirely faded	Faded	Hardly faded	Absent	Faded	Present
2	X			X			X		
1		X		X			X		
1			X			X	X		
3			X		X			X	
1		X		X				X	
6			X		X				X
12			X			X			X

compact digestive gland, which occupies around two-thirds of the whole body cavity. No distinct stomach is detectable within the digestive gland; a caecum is absent. The intestine originates dorsally from the posterior third of the digestive gland and encircles the heart in a wide loop. The distal intestine runs posteriorly on the right side and ends medio-dorsally in the prominent anal papilla. The anal cone is situated in the center of a small cavity within a large tubercle, which dorsally has a round opening.

**Central nervous system (CNS; Figure 4):** The CNS is positioned dorsally on the pharyngeal bulb. The cerebropleural ganglia are completely fused. The visceral loop is short, without distinct ganglia. The rhinophoral ganglia are separate, attached to the cerebral ganglion. The optic nerves are around two times as long as the diameter of the eyes. The pedal ganglia are situated next to the cerebropleural complex with the statocyst nestling in between. The buccal ganglia are adjacent to the ventrolateral surface of the esophagus, posterior to the central nerve ring. A small gastroesophageal ganglion is intimately attached to each buccal ganglion.

**Reproductive system (Figure 5):** The flat gonad overlies the anterior part of the digestive gland, being covered by the kidney dorsally and laterally. The triaulic anterior genitalia are situated in the space between the pharyngeal bulb and the digestive gland. The thin hermaphroditic duct passes into the spherical, brown colored ampulla which is faded to cream-white in some preserved speci-

mens. The postampullar gonoduct is short, dividing into the vas deferens and oviduct, the latter entering into the female glands. The vas deferens enlarges into a convoluted prostatic portion which extends to considerable length in larger specimens and distally narrows again into a muscular ejaculatory portion. The penis bears several rows of cuticular spines and enters into a common vestibulum with the vagina. The vagina is a narrow, rather long and straight duct which leads into the sperical, thin-walled bursa copulatrix. Next to the insertion, the vaginal duct arises from the bursa, bearing a stalked, muscular, elongate-ovate receptaculum seminis. The vaginal duct enters into the female gland mass close to the nidamental opening.

**Circulatory and excretory system:** Like all phyllidiids, *P. varicosa* possesses secondary gills situated ventrolaterally, in the groove between notum and foot. The flat, triangular shaped, grey gill leaflets are interrupted by the mouth anteriorly and the reproductive openings on the right side. Large and small gill leaflets alternate more or less regularly. The circulatory system corresponds to the description and drawings of *Phyllidia flava* Aradas, 1847 (as *Phyllidia pulitzeri* Pruvot-Fol, 1962) by Wägele (1984). The heart is placed mediodorsally on the digestive gland and kidney, in the posterior half of the body. Only two lateral vessels enter into the wide atrium. The muscular ventricle is situated anterior to the atrium. The large aorta runs to the blood gland which overlies the esophagus and parts of the reproductive organs. The blood gland

Figure 1

*Phyllidia varicosa*, external variation of preserved specimens. A. Entirely faded specimen (29 mm; ZSM No. 19983418) with continuous tubercle ridges, dorsal view. B. Entirely faded specimen (29 mm; ZSM No. 19983418), ventral view. C. Hardly faded specimen (25 mm; ZSM No. 19983420) with broken tubercle ridges, dorsal view. D. Hardly faded specimen (25 mm; ZSM No. 19983420) with unbroken foot stripe, ventral view. E. Hardly faded juvenile specimen (13 mm; ZSM No. 19983421) with a single tubercle ridge, dorsal view. F. Hardly faded juvenile specimen (13 mm; ZSM No. 19983421) with unbroken foot stripe. Scale bar = 1 cm.

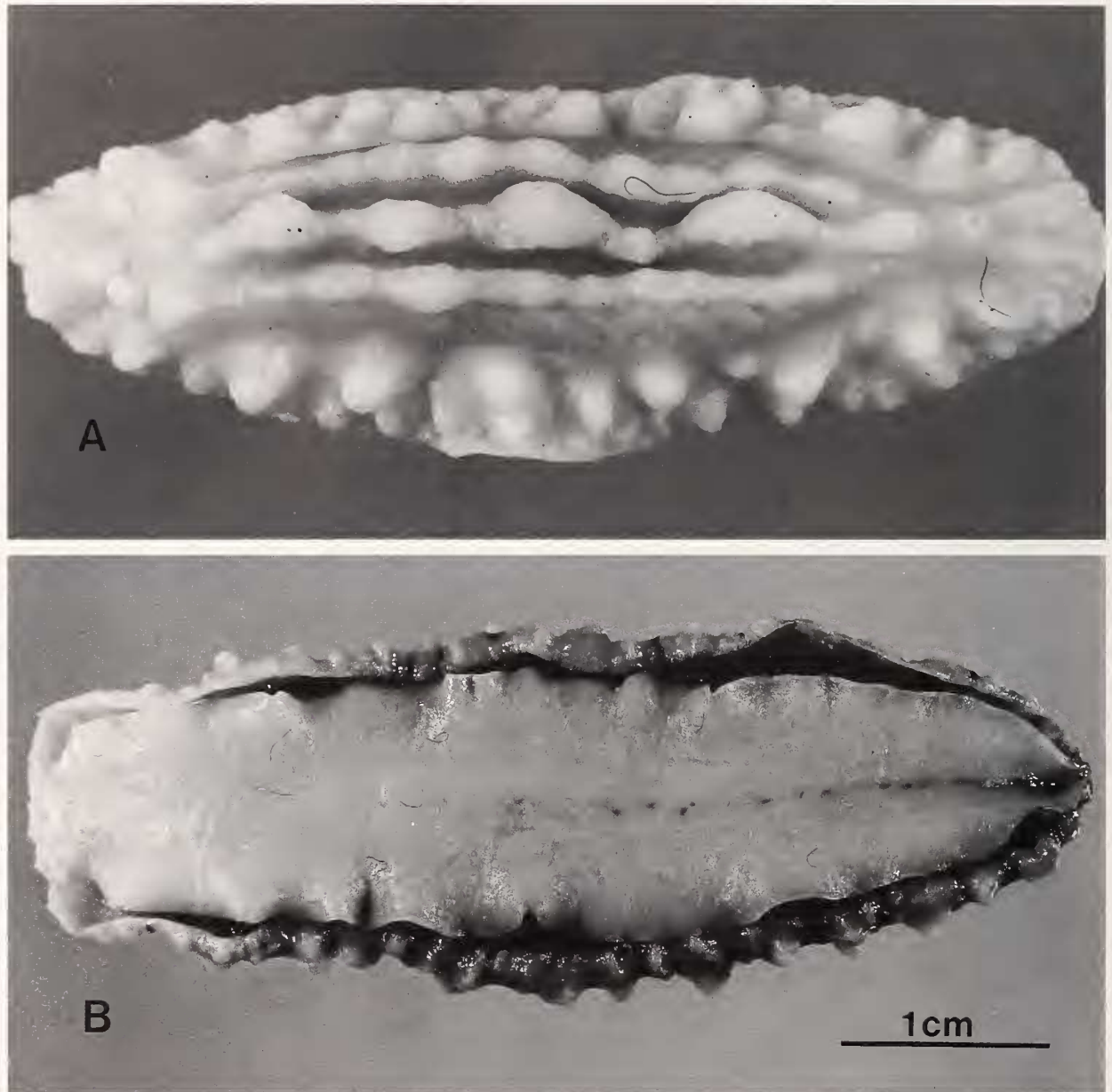


Figure 2

*Phyllidia varicosa*, partly dissected specimen (53 mm; ZSM No. 19983422) showing a transitional stage of fading due to preservation. A. Dorsal view. B. Ventral view; the black foot stripe has disappeared except for some small remainders. Scale bar = 1 cm.

is a rounded to an elongate lobe which differs considerably in size. The syrinx is situated posteroventrally to the wide pericard, at the right side. The flat kidney covers the ovotestis dorsally and laterally.

**Mantle:** The notum is thick and very tough. Basally, it is strengthened by a cross lamellar layer of strong, needlelike spicules. From this layer, spicules arranged like

bunches of flowers rise into each single tubercle; these structures are absent in areas between the tubercles. The spicules, reaching up to 1 mm in length and around 50  $\mu\text{m}$  in diameter, are hollow, and all consist of calcium-carbonate. Silicate or chitinous elements mentioned by Brunckhorst (1993) were not detected within the notum. Upper notum layers have a spongelike consistency and contain many large subepidermal glands.

## DISCUSSION

The 26 Indonesian specimens examined correspond to the description of *P. varicosa* by Brunckhorst (1993). These specimens, all fixed and preserved in the same way, show that even a complete loss of black pigmentation may be caused by preservation (see Table 1). Yonow (1996) stated that she had "yet to see a *P. arabica* which is so faded that the black on the dorsal and ventral surfaces disappears completely" and emphasized that preserved phyllidiid specimens retain their black coloration for very long periods. Most of the examined *P. varicosa* specimens after 4 years of preservation indeed still possess a very distinct black line on the foot sole (see Table 1, Figure 1D, F). However, four specimens lost this line, which had been present in life and in a freshly preserved state. Two of these specimens even faded completely and are entirely whitish now (see Figure 1A, B) due to preservation artifacts.

According to Yonow (1986, 1988, 1996), the only difference between the two species *P. varicosa* and *P. arabica* is the absence vs. presence of a black stripe on the foot sole. Yonow had no example of a specimen without such a stripe, but based her theory of two separate species on Cuvier's (1804) preserved holotype specimen of *P. varicosa*, considered lost for a long time. The rediscovery of this holotype in 1998 finally proved that *P. varicosa* has to be regarded as the valid name for the common Indo-West Pacific species with a longitudinal black foot stripe and that *P. arabica* is a junior synonym (Willan et al., 1998). Although collected more than 200 years ago, the holotype still possesses a line of very faded dark dashes on the foot sole. In the literature there are only three other descriptions of *P. varicosa* lacking a foot stripe (Gray, 1857; Quoy & Gaimard, 1832; Vayssi re, 1912; see Yonow, 1986), all referring to preserved specimens. In contrast, numerous authors mentioned specimens with a black foot stripe collected all over the Indo-Pacific region (see Brunckhorst, 1993; Yonow, 1986). The present study shows that it is inappropriate to use the black foot stripe to separate preserved phyllidiid specimens as it can fade partly or entirely, regardless of the state of fading of dorsal pigmentation (Table 1); in particular, *P. varicosa* from the Red Sea lost the black foot

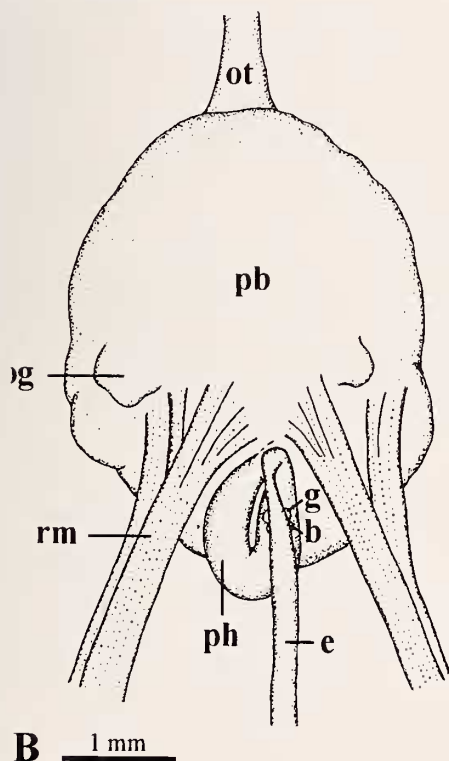
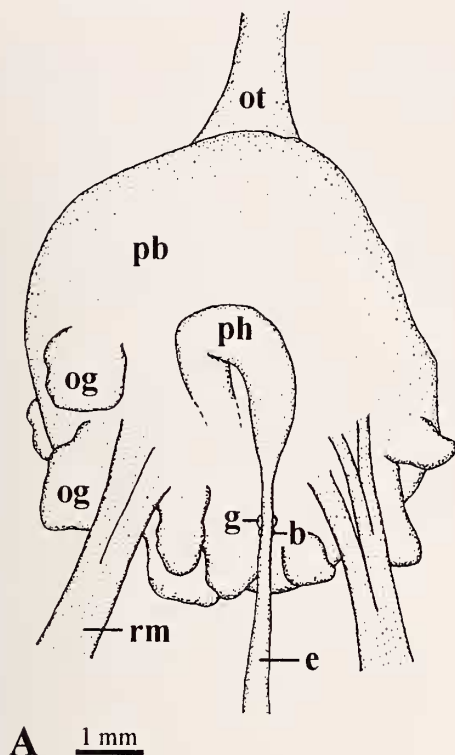


Figure 3

*Phyllidia varicosa*, variability of the anterior digestive system. A. Large specimen (ZSM No. 19983422) with well-developed oral glands and a simple pharynx loop. B. Smaller specimen (ZSM No. 19983419) with less developed oral glands and a pharynx forming an "S" bend. Scale bars = 1 mm. Key: b, buccal ganglion; e, esophagus; g, gastroesophageal ganglion; og, oral glands; ot, oral tube; pb, pharyngeal bulb; ph, pharynx; rm, retractor muscles.



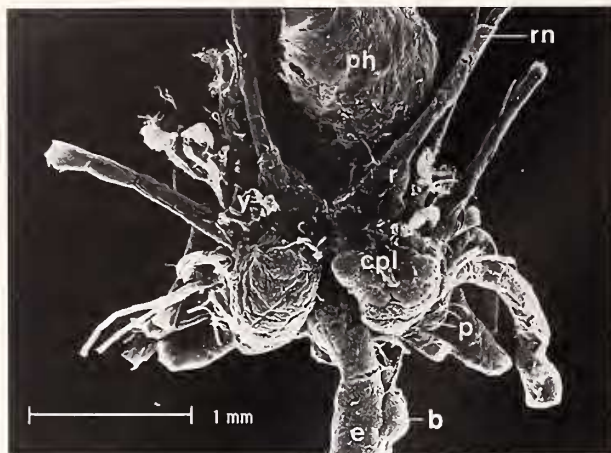


Figure 4

*Phyllidia varicosa* (ZSM No. 19983422), SEM micrograph of the CNS. Scale bar = 1 mm. Key: b, buccal ganglion; cpl, cerebropleural ganglion; e, esophagus; p, pedal ganglion; ph, pharynx; r, rhinophoral ganglion; rn, rhinophoral nerve; y, eye.

stripe in less than 1 year while retaining the black notum coloration.

*Phyllidia varicosa* displays considerable individual variation in both external morphology and anatomy. This also refers to features used by Yonow (1996) to distinguish the new species *P. alyta* Yonow, 1996, from *P. varicosa*. The black pigmentation on the foot sole of both *P. varicosa* and *P. alyta* does not always form a dotted line but is often an unbroken stripe (see Yonow, 1996: fig. 9 C, D; this study, Figure 1D, F). The four longitudinal black lines on the dorsum of *P. varicosa* do not always touch. There are also *P. varicosa* specimens with four individual lines or specimens with only the two inner lines being connected (this study). However, the recently collected specimen and the re-examined type and museum material from the Maldives clearly show the unique dorsal color pattern of *P. alyta* and highlight the differences to *P. varicosa*: *P. alyta* completely lacks blue-grey coloration; its background color is white. The two inner of four black longitudinal stripes on the dorsum are always connected by a short transverse line between the rhinophores (Yonow, 1996:fig. 9A; this study) which is absent in *P. varicosa*. Very few small black dots occur on the white mantle margin of *P. alyta*; black lines running to the edge, which are typical for *P. varicosa*, are absent. The rounded tubercles are arranged in seven distinctive rows (see Yonow, 1996:fig. 9A; this study), of which only the inner three form crests similar to those in *P. varicosa*. The genitalia of *P. alyta* generally agree with those of *P. varicosa* (see Figure 5). However, the bursa copulatrix of *P. alyta* possesses a distinct stalk, while the vagina and vaginal duct have a common insertion at the base of the bursa in *P. varicosa* (i.e., the bursa is not

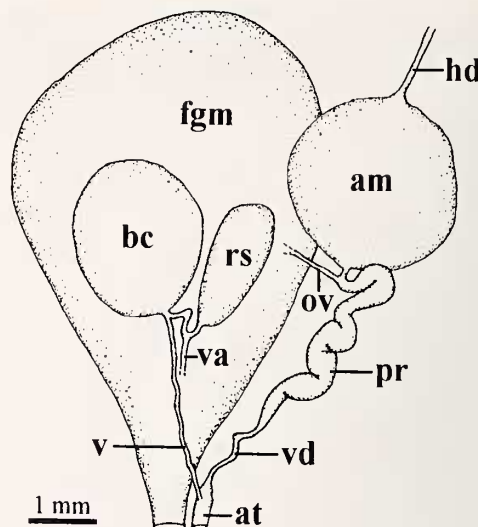


Figure 5

*Phyllidia varicosa* (ZSM No. 19983422), reproductive system. Scale bar = 1 mm. Key: am, ampulla; at, common atrium; bc, bursa copulatrix; fg, female gland mass; hd, hermaphroditic duct; ov, oviduct; pr, prostatic vas deferens; rs, receptaculum seminis; v, vagina; va, vaginal duct; vd, muscular vas deferens.

stalked) and, according to Brunckhorst (1993), in all other *Phyllidia* species. Moreover, seven dissected specimens of *P. alyta*, ranging from 21 mm to 27 mm preserved body length, are all sexually mature. In contrast, the female gland mass is not yet developed in *P. varicosa* specimens smaller than 40 mm preserved body length. With a known living maximum length of 40 mm (Yonow, 1996), *P. alyta* is much smaller than *P. varicosa*, reaching up to 115 mm (Brunckhorst, 1993).

Other anatomical features do not differ significantly. The pharyngeal bulb, according to Yonow (1996) symmetrical in *P. varicosa* and asymmetrical in *P. alyta*, is variable in both species (Brunckhorst, 1993:fig. 4; this study) and highly influenced by the degree of development of oral glands. Bergh (1869) used foregut symmetry to contrast the "general symmetrical" foregut of the genus *Phyllidia* from the long, highly folded, and therefore asymmetrically shaped foregut of *Phyllidiella* Bergh, 1869, but not to distinguish between different *Phyllidia* species. Within *Phyllidia* we agree with Marcus & Marcus (1970) and Brunckhorst (1993) in considering details of foregut symmetry an unreliable character. Showing remarkable intraspecific variability, the pharynx of *P. varicosa* may be a rather narrow tube as claimed for *P. varicosa* by Yonow (1996) or considerably swollen as in *P. alyta*. The pharynx either forms a large loop to the anterior-right (Brunckhorst, 1993:figs., 4, 5; this study, Figure 3A) or describes an "S" bend posteriorly (Brunckhorst, 1993:fig. 22; this study, Figure 3B) before passing the central nerve ring. The different conditions may re-

flect different ontogenetic stages, since specimens with a pharynx forming an "S" were small and immature, while specimens with a pharynx-loop were all mature. At their insertion, the ribbon like pharyngeal bulb retractor muscles of *P. varicosa* may split into smaller bundles (this study, Figure 3), as described for *P. alyta* by Yonow (1996). The oral tube was not uniformly colored in the six *P. alyta* specimens anatomically examined by Yonow (1996); it was marked by black lines, a few black spots, or black pigmentation was completely absent as in *P. varicosa*.

In conclusion, *P. varicosa* and *P. alyta* cannot be distinguished based on foregut anatomy or the appearance of the foot stripe, but with dorsal color pattern, arrangement of allosperm receptacles, and body size. Specimens from Mauritius assigned to *P. alyta* by Yonow (1996) differ from both the type material of *P. alyta* and from *P. varicosa* due to their dense notal tuberculation and dorsal color pattern; thus, their identity cannot be evaluated here.

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